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# *Espeletia* giant rosette plants are reliable biological indicators of time since fire in Andean grasslands

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## 1 Abstract

Páramo grasslands in the tropical Andes are fire prone ecosystems and an understanding of their fire ecology is fundamental to biodiversity conservation and ecosystem management. Fire registers are normally impractical in these remote, cloud-covered landscapes, but *Espeletia* giant rosette plants have been proposed as biological indicators of time since fire in páramos. *Espeletia* giant stem rosettes tolerate fire well, protecting apical buds in at the heart of their leaf rosettes, and for some species, germination is known to be enhanced by fire. As the plant grows, its dead leaves remain attached to the stem, but fire removes these and resets the "leaf clock". This study uses a unique register of fires in one Ecuadorian páramo to assess the robustness of this biological indicator. Dead leaf cover on *Espeletia pycnophylla* giant rosette plants was measured in fifteen different sites with known fire dates from 2000 to 2014. The growth rates of plants at four different elevations were measured over a two-year period and used to estimate time since fire based on dead leaf cover in the known sites. Estimates were accurate to ± 2 y. Thus, where fire records are missing, relatively easy measurements of growth rates and dead leaf cover of *Espeletia* giant rosette plants can provide reliable estimates across a wide range of times since fire. This approach has value for direct investigations into fire ecology but also for studies in which controlling for fire dynamics is necessary to reveal underlying patterns. Therefore, this approach also offers a means to obtain better information on other landscape-scale processes such as the impact of climate change on biodiversity or the provision of ecosystem services.



Key words: páramo, burning, growth rates, fire regimes, fire history, landscape ecology


## 2 Introduction

Fires occur in nearly every terrestrial biome on Earth, simply because wherever vegetation grows there is the potential for it to burn (McKenzie et al. 2011). Fires represent a 'punctuated' form of disturbance and can instantly 'reset' vegetation succession, plant

community composition, species dominance, and spatial patterns (McKenzie et al. 2011; Ramsay 2014). These drastic effects of fire are not always aligned with and can conceal the subtler signals of more continuous ecological processes, such as climate change. Understanding fire regimes and the current stage of vegetation in the fire recovery cycle is crucial to separate fire responses from longer-term ecological trends and thus facilitate investigations into the general response of biodiversity to environmental change in fire prone ecosystems. Satellite imagery and remote sensing have revolutionized the study of fires in landscapes, but are not feasible methods in some cases where cloud cover and lack of resources limit these technology dependent methods (Ramsay 2014). It would be useful to have a simple, on the ground method to reconstruct recent fire history. It has been proposed that plants might provide a way of estimating time since fire, if their growth after fire is predictable.

Tropical alpine regions support fire-prone ecosystems in which the lack of fire records hampers studies into fire ecology, biodiversity conservation and management, and the monitoring of climate change. Tropical alpine ecosystems occur in the upper regions of the Andes, the Afroalpine belt and to a lesser extent, Indonesia and Papua New Guinea (Buytaert et al. 2011). The high altitude grasslands of the Northern Andes, known as *páramos*, are the largest extension of tropical alpine ecosystems, covering an area of around 35,000 $km^2$ (Madriñán et al. 2013). The páramos are hotspots of biodiversity and endemism (Myers 2006) and provide essential ecosystem services, such as water provision and carbon storage (Buytaert et al. 2011) that sustain biological processes on both local and global scales, and support the livelihoods of millions of people (Buytaert et al. 2006). Global climate change is predicted to displace ecosystem boundaries and the increased isolation of remaining páramo patches is expected to induce species extinction and biodiversity loss (Buytaert et al. 2011). Drier and warmer soil conditions are predicted to cause faster organic carbon turnover, decreasing below ground organic carbon storage. These changes may have major impacts on water supply (Buytaert et al. 2011). Thus, conservation and sustainable management of the páramo is vital.

Páramo landscapes have been burned regularly by people for thousands of years (Laegaard, 1993; Horn & Kappelle, 2009). The páramos are used extensively for grazing of livestock, and burning of vegetation encourages new, more nutritious growth for grazing (Laegaard 1992; Ramsay & Oxley 1996). The frequency of burning depends on vegetation recovery but is typically every 2 to 5 years (Ramsay & Oxley 1996). Accidental fires have increased as visitor numbers have grown in recent decades (Ramsay 2001). These fires play an intrinsic ecological role in the páramo and local fire regimes have been shown to impact biodiversity, vegetation composition and ecological dynamics, agricultural production, soils, and hydrology (Ramsay 2014; Sklenář & Ramsay 2001). The páramos contain a wide array of specialized plant species extraordinarily well adapted and resilient to fire (Laegaard 1992). Fire disturbance creates a competitive advantage for those plants with suitable adaptations and without doubt determines the detail of biodiversity composition and ecological dynamics of modern páramo grasslands (Horn & Kappelle 2009; Ramsay 2014). A better understanding of the nature of fire regimes, the ability and time needed for páramo plant communities to recover from burning, and the impacts of fire on ecosystem service provision is essential to determine whether management decisions are beneficial from an ecological perspective (Hardesty et al. 2005).

Unfortunately, investigations of post-fire dynamics in the páramo are limited by the lack of information about fire history. Fire records are very rarely kept, and even when they are, they are incomplete. Monitoring fires on the ground is difficult in the remote and rugged páramos, and high cloud cover limits remote sensing and satellite imagery methods of assessment (Ramsay 2014). The use of ecological indicators has been proposed as a possible approach to determine time since fire at a landscape scale in the páramo. In Costa Rican páramos, the growth rings of certain shrubs can be used to date fires (Horn 1989; Kerr et al. 2017; Williamson et al. 1986), but this approach is limited in the páramos of northern Ecuador because shrubs do not reliably form annual growth rings there (personal observation by authors). Garcia-Meneses and Ramsay (2014) investigated the use of *Puya* giant rosettes plants to estimate time since fire. Pulses of recruitment of *Puya* occur soon after fires and result in a cohort of plants of the same age. However, there was found to be

a large margin of error as the recruitment pulse may take place within a window of several years after fire.

Ramsay (2014) proposed that *Espeletia* giant rosette plants have potential to indicate recent fire history more accurately. *Espeletia* giant rosettes are characteristic plants of the Northern Andes (Diazgranados 2012) and of ecological importance because they represent a large proportion of the biomass in páramo ecosystems, help to regulate the hydrological cycle, and prevent soil erosion (Garcia et al. 2004). The subtribe Espeletiinae currently has eight recognized genera, 141 species, and 17 subspecies (Diazgranados 2012). *Espeletia* cover large areas of the páramos of Colombia, Venezuela and northern Ecuador (Diazgranados 2012; Luteyn et al. 1992), with the potential to act as an indicator of time since fire throughout these grasslands. *Espeletia* giant rosettes have a peculiar morphology, specifically adapted to the high elevation and harsh climate of the tropical mountain environment (Carlquist 1994; Ramsay 2014). *Espeletia* are very resilient to fire, protecting apical buds in giant leaf rosettes lifted above the ground (Laegaard 1992). Ramsay (2014) documented mortality of adult *Espeletia* plants at 2.5% in unburned vegetation, but higher after burning (8% for a low intensity fire to 56% for a very high intensity fire). Germination of some species eg. *Espeletia pycnophylla* is known to be enhanced by fires due to the availability of open space, light and nutrients (Laegaard 1992; Suárez & Medina 2001). Many species of *Espeletia* retain dead leaves on the stem (known as marcescence), which serve to insulate the water reserve inside the plant during cold nights (Goldstein & Meinzer 1983). These marcescent leaves are normally burned away during a fire, but clothe the stem that grows afterwards. If the stem growth rate of the population is known, then the time taken to grow the stem that appears after a fire can be calculated—a kind of “leaf clock”.

This study builds upon Ramsay’s (2014) proposal, seeking to test the effectiveness and limitations of the approach and to refine it across a wide range of study sites and times since fire. A unique set of historical fire dates since 2000 has been recorded for the páramo of El Ángel and Volcán Chiles, northern Ecuador, which is dominated by *Espeletia pycnophylla* Cuatrec., a species typical of the páramos of this region, including parts of southern Colombia (Diazgranados 2012). We compared recorded fire dates with time-since-

fire estimates, based on *Espeletia* leaf cover and growth rates, to check the accuracy and robustness of the indicator approach. For the longer-term, we wanted to demonstrate the use of *Espeletia* species more generally to assess recent fire histories in páramos across the northern Andes, in order to inform sustainable management of these important ecosystems, and to promote the use of plants as indicators of fire in ecosystems around the world.

# 3 Methods

## 3.1 Study areas

The Reserva Ecológica El Ángel (REEA) is part of the Ecuadorian system of protected areas, and is managed by the Ministry of Environment. The reserve was set up to protect semi-natural and natural ecosystems (mostly high-altitude páramo grasslands) and is surrounded by landscapes where agriculture is the main land use. Contiguous with the northern boundary of the REEA is the páramo of Volcán Chiles, now managed as a private reserve by the Comuna Esperanza, historically a farming cooperative, based in nearby Tufiño. Like most páramo grasslands in Ecuador, fires have been frequent in REEA and Volcán Chiles in recent decades. Typically, fires have been set to improve livestock forage, to facilitate hunting, or by accident (Ramsay 2001). Concerned by the potential ecological damage caused by these fires within the reserve, the Pontificia Universidad Católica del Ecuador carried out two studies with help from park officials and local fire brigades, and technical assistance from Randi Randi, an NGO. The first project created an inventory of known fires from 2000–2008 (Valdospinos Navas 2008), while the second established a protocol for registering fires after 2008 (Bustos Insuasti 2008). These projects also included the páramo beyond the strict limits of the reserve itself in the agricultural buffer zone. As a consequence, good quality information exists in and around REEA about known fire dates in particular places. Before 2008, these dates were recorded only at the level of year, but subsequently precise dates have been recorded. The information is not comprehensive, in that some fires might have occurred without being recorded, especially smaller ones, but many fires have been noted. These records appear to be unique in the páramos for this span of time and represent a valuable resource for studying the effects of fire on this ecosystem.

To establish whether *Espeletia* giant rosette plants can be used to successfully estimate time since fire, fifteen locations on the Western Cordillera within REEA and its buffer zone were selected to represent a range of times since fire (burned from 2000–2014, representing <1 to 15 y ago at the time of survey) at elevations of 3500–3900 m. All were within two hours' walking access from a road, for logistical reasons as well as the likelihood that fire records nearer to the roads would be more comprehensive than in less frequently visited, remote places. Each fire site was located with GPS coordinates obtained from the records.

More recently, the fire brigade in San Pedro de Huaca, Carchi, Ecuador, has also begun recording fires in páramo grasslands on the Eastern Cordillera in northern Ecuador. Three additional sites were included from the páramo of La Bretaña, all at elevations of 3600–3750 m and burned within 2½ years of the survey.

The páramo grasslands in the study areas were dominated by *Calamagrostis* tussock grasses and giant rosettes of *Espeletia pycnophylla* Cuatrec. This species of *Espeletia*, like many others in the northern Andes, retains marcescent leaves on the stem. These plants are found at high densities throughout these páramos, counted at 1300–5400 adult plants $ha^{-1}$. Some plants achieve heights of more than 4 m, but most die or fall over before they reach that size.

### 3.2 Field measurements and data analysis

Growth rates of *Espeletia* plants were measured from March 2012 to March 2014. At the start of the period, ten plants approximately 1 m tall were randomly selected at each of four elevations on Volcán Chiles (3600, 3800, 4000, and 4200 m) and the well-defined lower limit of the living rosette was marked with string around the stem. Close to two years later, the difference between the string and the new lower limit of the living rosette was measured to the nearest centimetre. From these measurements and the time difference between observations, mean annual stem growth rates were calculated for each elevation.

At each of the fifteen fire sites, we randomly selected 50 *Espeletia* plants with a lower limit of marcescent leaf cover 1–1.5 m above the ground. This indicated that these plants would have been 1–1.5 m tall at the time of the last fire, a height which showed consistent leaf removal by flames in an earlier study (Ramsay 2014). The marcescent leaf cover of each

plant was measured: the length of stem with accumulated dead leaf blades (not leaf bases alone) from their attachment point on the stem to the base of the living rosette (Fig. 1). In rare cases of asymmetrical fire damage, measurement was always taken from the side of the plant where the fire burned highest on the stem.

The mean growth rates and dead leaf cover were combined to estimate time since fire. Simply, the height of stem with marcescent leaves attached was divided by the growth rate to give the number of years needed to grow that amount of stem. Ramsay (2014) suggested an adjustment to correct for unrepresentative growth rates during an initial period after the fire. However, we did not apply such an adjustment in this study. Although there might be potential for underestimating time since fire, because the rosettes might have initially grown more slowly as they recovered from the fire, an overestimation is also possible, since green leaves in the living rosette are often killed but not destroyed by the fire. The marcescent leaves formed by these leaves do not indicate post-fire regrowth. The balance between these processes of under- and overestimation is unknown at present, and so no attempt was made to adjust estimates in this way.

Ramsay (2014) also recommended removing the greatest and lowest 10% of marcescent leaf cover measurements from a 50-plant sample, leaving an 80% core of 40 plants. This was intended to remove outliers of unusual fire experience or subsequent regrowth from the calculations. To explore further the effect of this approach, the consistency of marcescent leaf cover measurements was evaluated by comparing leaf cover statistics for a range of different subsample sizes from the 50 measured plants at each site (all plants; 96%; 80%; 60%; 40%). A check was also made to see if variability in dead leaf cover within populations at each site changed predictably with time since fire.

Ultimately, a comparison was made between known times since fire—from the records—and those estimated from marcescent leaf cover. Standard statistical tests were performed with IBM SPPS statistics for Macintosh (Version 23, Armonk, New York, USA).

# 4 Results

*Espeletia* annual growth rates fell into two groups: plants at 3600 and 3800 m elevations grew at just over 9 cm $y^{-1}$, while plants at 4000 and 4200 m grew 2–3 cm $y^{-1}$ less (Kruskal-Wallis $X^2$= 35.908, df = 3, $p < 0.001$; Fig. 2). At 3600 m elevation, the mean growth rate of *Espeletia* plants was 9.28 cm $y^{-1}$. This figure was used to calculate estimates of time since fire for all but one of the plots, since they were located at similar elevations. One plot was located at 3900 m, so a different figure of 7.89 cm $y^{-1}$ was used for the calculations there.

Marcescent leaf cover on *Espeletia* stems was measured for 50 plants at each of the sites. Table 1 presents five options for calculating the mean for use in the subsequent estimates. With no or few outliers removed (all or 96% subsamples), the higher variability among the plants at a site made distinguishing between sites less clear-cut (indicated by the multiple comparison of means tests). With a larger number of plants excluded from the extremes (60% and 40% subsamples), distinguishing between sites became compromised by the smaller sample size. The most effective option was removing five plants from each extreme of the distribution (80% subsampling). This was the option used to calculate the estimates that follow.

As time since fire increased, mean marcescent leaf cover increased predictably (regression: $F_{1,14}$=82.51, $p$<0.001; Fig. 3A). In addition, the variability of mean marcescent leaf cover also increased predictably (regression: $F_{1,14}$=21.69, $p$<0.001; Fig. 3B).

Estimates of time since fire made on the basis of marcescent leaf cover matched well with known fire dates (regression: $F_{1,14}$=115.96, $p$<0.001; Fig. 4), with 14 out of 15 fire sites within 1.8 years of the known fire date.

# 5 Discussion

*Espeletia pycnophylla* marcescent leaf cover showed predictable growth after fire, and measurements of marcescent leaf cover in known sites provided effective estimates of time since fire, up to 15 years after fire. The use of *Espeletia*'s "leaf clock" for estimating when the last fire happened at a particular site seems to be reliable well within the timeframe of

typical fire cycles in the páramo grasslands of the northern Andes, normally at intervals of 2–5 years (Keating 2007; Ramsay & Oxley 1996).

However, the variability of marcescent leaf cover increased as time since fire elapsed. The standard deviation of marcescent leaf cover measurements reached the equivalent of 8–9 months of growth by 5 y after a fire, and just over two years of growth by 15 y after a fire. This is an acceptable level of error, where no other means of estimating time since fire exists, and is consistent with the concept of a population where individual growth rates vary slightly from plant to plant. As time goes by, these differences accumulate and variation in marcescent leaf cover increases within a sample of plants. Microtopographic factors might promote or restrict growth of individual plants, for example by affecting water availability (Pérez 1987). Competition with neighbours and genetic variation could also contribute to individual growth rate variability. *Espeletia* height has also been shown to affect individual growth rates (Ramsay 2014). As plants grow taller, night-time rosette temperatures decrease and slower metabolism, even damage to the plant's apical meristem, becomes more likely. However, at lower elevations, this is likely to be outweighed by warmer temperatures and improved daytime growth. *Espeletia* plant stems hold an inner reservoir of water that, insulated by the marcescent leaves, provides a supply of unfrozen water to the leaves in early morning when soil water is potentially still too cold to be of use (Goldstein & Meinzer 1983). Therefore, as time passes after a fire, surviving *Espeletia* plants at the elevations studied here would be expected to increase in growth rate as they grow taller—and this might also contribute to the increased variance in leaf cover over time.

To some extent, the variability in individual growth rates can be taken into account by removing outliers with particularly rapid or slow growth, compared with the more general population. In this study, we followed Ramsay's (2014) original proposal for including only a core 80% of 50 plant measurements. It did provide a suitable protocol for removing unusual outliers, while maintaining an appropriate sample size. Apart from the reasons noted above, outliers are also likely in variable, low intensity, fast moving fires that occasionally miss entire plants, leaving their leaves intact (Ramsay, 2014). Since this situation does not always reflect the fire conditions, it is not surprising that excluding outliers did not make much of a

difference to the mean estimates of most sites. Nevertheless, excluding outliers routinely does provide some confidence that the potential impact of this issue would be addressed. Furthermore, in cases of asymmetrical marcescent leaf cover, the accuracy of our estimations suggests that measuring the side of plant where the fire burned highest on the stem was an effective approach.

In addition to differences in leaf cover between plants within a site, there are likely to be variations in growth rate between sites, at the population level. The intensity of the fire might have an impact on the recovery and subsequent growth rates of surviving plants. Fires burning upslope, with the wind, are likely to be of low intensity, burning quickly and lightly across the area. The vegetation would be damaged less and likely to recover more quickly. Some *Espeletia* plants might be missed by such fires altogether. Contrastingly, slowly burning, intense fires might result in high levels of mortality and much longer periods of reduced growth afterwards. For example, the time since fire of one of the sites included in this study was not estimated well. The site was known to have been burned 9 years before the observations were made, but leaf cover measurements overestimated this time by nearly three years, suggesting growth rates were faster at this site. The site was located on steep slope and the vegetation was unusually dense, with tall shrubs and tussock grasses. The slope and topography could have created conditions for a low intensity fire. We found a high standard deviation of leaf cover measurements at this site, consistent with the expectations of a low intensity fire.

Elevation strongly influenced *Espeletia* growth rates. Growth rates varied from 6.64–9.28 cm $y^{-1}$, with a marked decrease between 3800 and 4000 m. *Espeletia* growth depends strongly on light and temperature. The moist adiabatic lapse rate is around 5–6 °C per kilometre increase in elevation, and would be expected to reduce growth rates. However, in these tropical mountains, soil temperature is strongly linked to solar radiation, which in turn is controlled partly by cloud cover. Based on observations in the study area over 25 y by one of the authors, the cloud base in the páramo of El Ángel and Volcán Chiles usually sits around 3900 m. Plants below the cloud base receive more light, while those above the line of the cloud base are in the cloud, resulting in foggy conditions with lower levels of light and

292 temperature. This helps to explain the marked decline in growth rate from 3800 to 4000 m.
293 Mountain topography can also affect growing conditions, such as that found at the 4100 m
294 road pass on Volcán Chiles from east (exposed, mostly cloudy) to west (sheltered, mostly
295 sunny). The growth measurements at 4200 m were made on the ridge in a zone where the
296 cloud dissipated as it began to descend down the western flanks of the mountain. *Espeletia*
297 growth was not significantly different at this elevation compared with plants 200 m lower
298 down the mountain in more constant cloud cover. These variations in plant response to
299 local conditions illustrate the value of measuring growth rates in a number of different
300 locations within a páramo landscape. Since these measurements only require some string, a
301 tape measure, and the ability to relocate marked plants at a future date, we recommend
302 collecting as much data on growth rate as is practical.

303 Another factor influencing growth rates is the variation in climate from year to year. In
304 particular, plant responses in the páramos have been linked to the El Niño Southern
305 Oscillation or ENSO (Luteyn 1999), which often results in less humidity in the mountains of
306 Ecuador and Colombia (Buytaert et al. 2006). In areas where water is not normally limiting,
307 plant growth could be promoted by the clearer skies. As an example, Ramsay (2014)
308 measured a mean *Espeletia* growth rate of 14.8 cm $y^{-1}$ at 3600 m elevation in northern
309 Ecuador , immediately after the 2009–2010 ENSO. This contrasts with the slower growth
310 rates of 9.28 cm $y^{-1}$ presented in this current study, from the same páramo and elevation,
311 but obtained over two years between ENSO events. It highlights the need to measure
312 growth rate over several years, and the need to consider the influence of climatic events like
313 the ENSO in interpreting variations in leaf cover in sites with different fire histories.

314 The success of using giant rosette marcescent leaf cover and growth rates to estimate time
315 since fire has important implications for future ecological research in the *Espeletia*-
316 dominated páramos of northern Ecuador and Colombia. To this point, investigations of fire
317 impacts have been limited by the absence of fire records. The ability to estimate time since
318 fire allows for more comprehensive investigations of the direct impacts of fire on plant
319 communities, soils, and water provision through time. Fire histories are also influential in
320 investigations of longer term changes in the páramo, such as the impact of climate change

or elevation on biodiversity. Fire causes greater shifts in both environmental conditions and plant community composition than the subtler effects of long term change. It is therefore important to know the stage of the fire cycle of each study site to control for the fire effects. This method will allow investigations to control for time since fire and will provide a means to carry out better studies in future (Ramsay 2014).

To encourage the use of this simple approach elsewhere in the northern Andes, we provide a protocol that explains clearly how to measure *Espeletia* growth rates and marcescent leaf cover (Online Resource 1). It includes examples of simple calibration graphs could be taken into the field for rapid assignment of a site to a time since fire. Similar calibration graphs could be developed for other páramos where fires are common.

Although this study was restricted to just one species of *Espeletia*, other species have potential as indicators, such as *Espeletia grandiflora* Humb. & Bonpl. in Colombia. Initial work with this species in Chingaza National Park has shown similar results to those published here, but more detailed studies should be carried out to confirm the suitability of this approach with other indicator species.

Of course, this approach to estimating time since fire is only directly applicable in regions with *Espeletia*. However, the principles of this indicator method may also have potential in the fire prone mountain grasslands of East Africa, where convergent evolution has produced a strikingly similar collection of plant forms (Smith 1994). The morphology, seedling establishment and growth of Andean *Espeletia* and East African *Senecio keniodendron* are remarkably alike, as are the life history strategies of Andean *Puya* (also with potential as a fire indicator) and East African *Lobelia* (Garcia-Meneses & Ramsay 2014).

Southern Ecuador, Perú, Costa Rica, and Panamá all have páramos with tussock grasses, but without *Espeletia* giant rosettes species. These regions have regular fire disturbance too, and face the same challenges of habitat conversion, climate change, and the need for sustainable management (Horn & Kappelle 2009). It would be useful to have a field method of indicating time since fire in these regions also. Tussock grass development through time after fire has potential in this regard, but other indicators should also be considered such as growth rings or zones in shrubs (Kerr et al. 2017).

While time since fire is a very important factor of fire regimes, it is not the whole story. This method of indicating time since fire from *Espeletia* marcescent leaf cover does not reveal the frequencies of fire events or the intensity of the last fire. Fire frequency, 'the number of fires per unit time in a particular stand of páramo' (Horn & Kappelle 2009), is thought to determine the vegetation structure and fuel availability of a site, influencing the spatial extent and intensity of fires (Keating 2007). Fire intensity is a very important factor of fire regimes and has been shown to have differential and significant impacts on the survival of plants during fire and the trajectory of plant community recovery. More research on fire frequencies and intensity is needed.

# 6 Conclusions

*Espeletia pycnophylla* marcescent leaf cover can be used as an effective indicator of time since fire in *Espeletia*-dominated páramo grasslands of Ecuador and potentially Colombia, given known growth rates. This approach is relatively inexpensive and simple, requiring no special equipment. Simple growth studies are needed to calibrate this method to local conditions. This indicator approach can be included in all future studies for which fire histories are influential. Relevant studies include direct investigations of the impacts of fire on biodiversity and vegetation recovery in the páramo. Indirect studies include those of the subtler impacts of longer term environmental change in the landscape, where signals of change are often confused by the more immediate effects of fire. The wider applicability of this indicator approach is to facilitate studies of fire effects on ecosystem services, such as water provision and carbon storage, in the páramo. Ultimately, this study contributes to the understanding of how fires can be included in management planning for these grasslands and how plants themselves can be used as biological indicators of fire.

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# 9 Tables

**Table 1.** Consistency of *Espeletia* leaf cover measurements with different subsampling of the complete sample. Mean ± standard error of marcescent leaf cover calculated for subsample sizes selected from the total of 50 plants of each site (all plants; 96%, 80%, 60%, 40%). Means sharing a letter were not significantly different according to a Student-Newman-Keuls test, following a Kruskall Wallace test (*df*=14 and $p < 0.001$ in every case).

| Time since Fire (y) | Observed Mean ± SE marcescent leaf cover in subsample | | | | |
|---|---|---|---|---|---|
| | **All (*n*=50)** | **96% (*n*=48)** | **80% (*n*=40)** | **60% (*n*=30)** | **40% (*n*=20)** |
| 0.5 | 10.7 $^{e}$ ± 1.5 | 9.5 $^{g}$ ± 0.7 | 8.9 $^{g}$ ± 0.3 | 8.9 $^{i}$ ± 0.2 | 9.0 $^{k}$ ± 0.2 |
| 1.6 | 12.4 $^{e}$ ± 0.7 | 12.1 $^{fg}$ ± 0.5 | 12.1 $^{fg}$ ± 0.4 | 12.0 $^{hi}$ ± 0.4 | 11.9 $^{jk}$ ± 0.3 |
| 2.4 | 17.4 $^{e}$ ± 0.4 | 17.3 $^{f}$ ± 0.4 | 17.2 $^{f}$ ± 0.3 | 17.0 $^{g}$ ± 0.2 | 16.9 $^{i}$ ± 0.2 |
| 2.4 | 15.5 $^{e}$ ± 0.6 | 15.4 $^{fg}$ ± 0.5 | 15.1 $^{f}$ ± 0.4 | 14.9 $^{gh}$ ± 0.3 | 14.8 $^{ij}$ ± 0.2 |
| 5.7 | 57.3 $^{d}$ ± 1.3 | 57.4 $^{e}$ ± 1.3 | 57.5 $^{e}$ ± 1.2 | 58.0 $^{f}$ ± 1.0 | 57.9 $^{h}$ ± 0.9 |
| 7 | 64.4 $^{cd}$ ± 2.3 | 64.4 $^{e}$ ± 2.2 | 63.8 $^{e}$ ± 1.9 | 63.8 $^{e}$ ± 1.7 | 64.6 $^{f}$ ± 1.4 |
| 8 | 63.5 $^{cd}$ ± 2.0 | 63.4 $^{e}$ ± 2.0 | 63.0 $^{e}$ ± 1.7 | 62.9 $^{ef}$ ± 1.2 | 62.8 $^{fg}$ ± 1.0 |
| 8 | 61.0 $^{d}$ ± 1.2 | 60.9 $^{e}$ ± 1.1 | 60.8 $^{e}$ ± 0.9 | 60.8 $^{ef}$ ± 0.7 | 60.3 $^{gh}$ ± 0.6 |
| 8 | 62.7 $^{cd}$ ± 1.3 | 62.7 $^{e}$ ± 1.2 | 62.6 $^{e}$ ± 1.0 | 62.5 $^{ef}$ ± 0.8 | 62.5 $^{fg}$ ± 0.8 |
| 8 | 81.7 $^{b}$ ± 2.1 | 81.1 $^{bc}$ ± 1.8 | 80.6 $^{b}$ ± 1.4 | 80.8 $^{b}$ ± 1.1 | 81.0 $^{c}$ ± 0.9 |
| 9 | 69.7 $^{c}$ ± 1.4 | 69.8 $^{d}$ ± 1.3 | 69.5 $^{d}$ ± 1.1 | 69.2 $^{d}$ ± 0.9 | 69.4 $^{e}$ ± 0.6 |
| 9 | 110.1 $^{a}$ ± 3.7 | 110.1 $^{a}$ ± 3.6 | 111.1 $^{a}$ ± 3.1 | 110.9 $^{a}$ ± 2.8 | 110.8 $^{a}$ ± 2.2 |
| 10 | 82.8 $^{b}$ ± 1.6 | 82.9 $^{b}$ ± 1.5 | 83.3 $^{b}$ ± 1.0 | 83.0 $^{b}$ ± 0.8 | 83.0 $^{c}$ ± 0.6 |
| 10 | 76.7 $^{b}$ ± 2.1 | 76.1 $^{c}$ ± 1.8 | 75.7 $^{c}$ ± 1.5 | 75.4 $^{c}$ ± 1.3 | 74.9 $^{d}$ ± 1.1 |
| 15 | 108.0 $^{a}$ ± 4.5 | 108.3 $^{a}$ ± 4.3 | 108.6 $^{a}$ ± 3.6 | 107.3 $^{a}$ ± 3.3 | 106.0 $^{b}$ ± 2.7 |

# 10 Figures

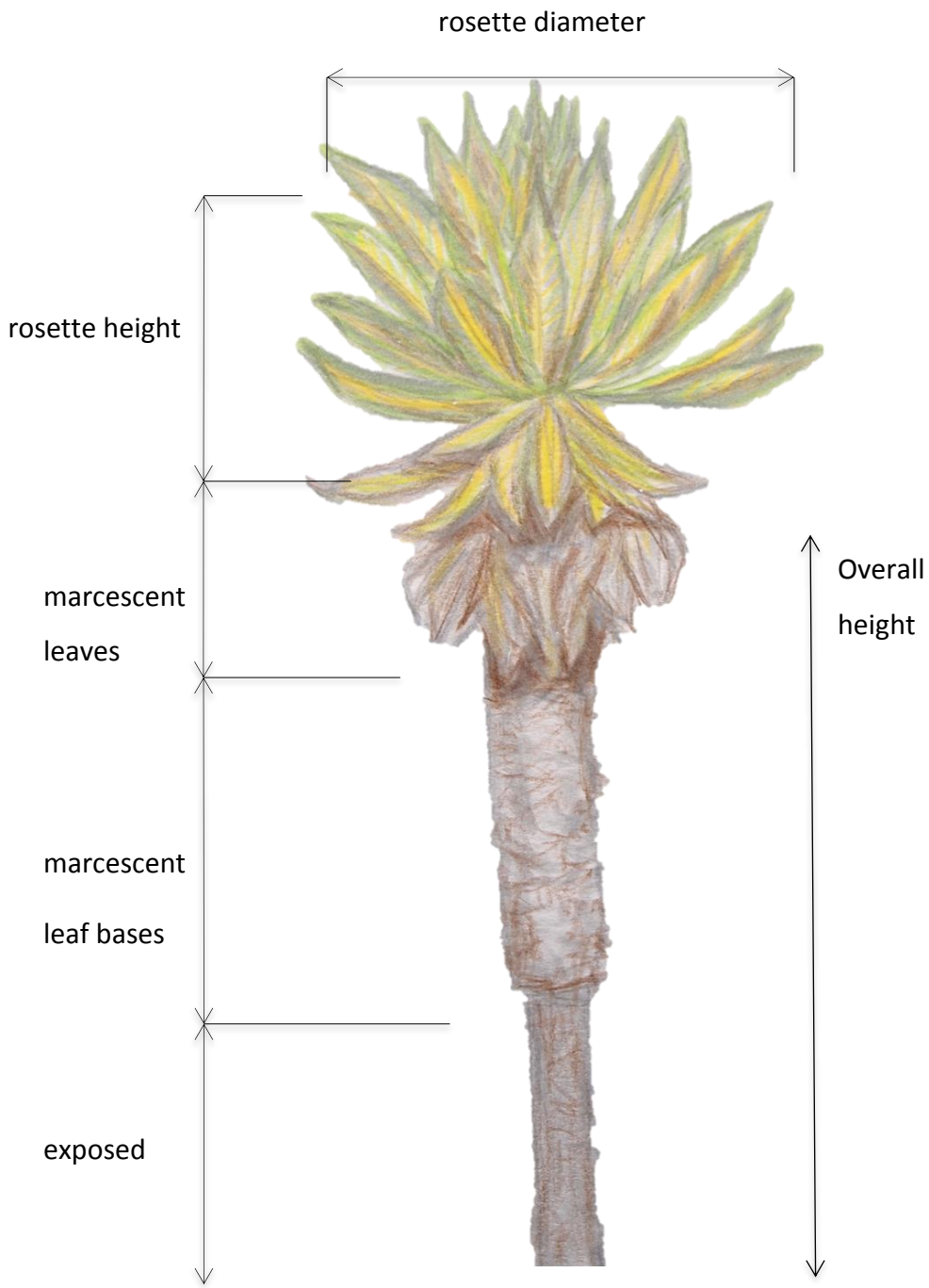
**Fig. 1.** Typical morphology of a burned *Espeletia pycnophylla* plant. Marcescent leaves remain attached to the stem beneath the living rosette leaves. Burning removes marcescent leaf blades and, after repeated fires, also removes the clasping leaf bases. The length of stem covered by accumulated marcescent leaves was measured in this study as an indicator of time since fire.

**Fig. 2.** Mean stem growth rates for *Espeletia pycnophylla* at four elevations on Volcán Chiles over a two-year period, 2012–2014. Error bars represent SE. Means sharing a letter were not considered significantly different according to a Student-Newman-Keuls multiple comparison of means test.

**Fig. 3.** Relationship between known time since fire and marcescent leaf cover of *Espeletia* plants at fifteen fire sites. (A) Mean marcescent leaf cover ($y$=4.39 + 7.88x; $r^2$= 0.864). (B) Variability (standard deviation) of marcescent leaf cover ($y$=0.42 +1.26x; $r^2$= 0.625). In both cases, statistics were calculated from 80% core subsamples of 50 plants, excluding five measurements from each tail of the distribution.

**Fig. 4.** Relationship between known and estimated time since fire for fifteen sites ($y$=0.06 + 0.93x; $r^2$=0.899). Calculated with growth rates of 9.28 cm $y^{-1}$ at 3600 m and 7.89 cm $y^{-1}$ at 3900 m.

485 Fig. 1

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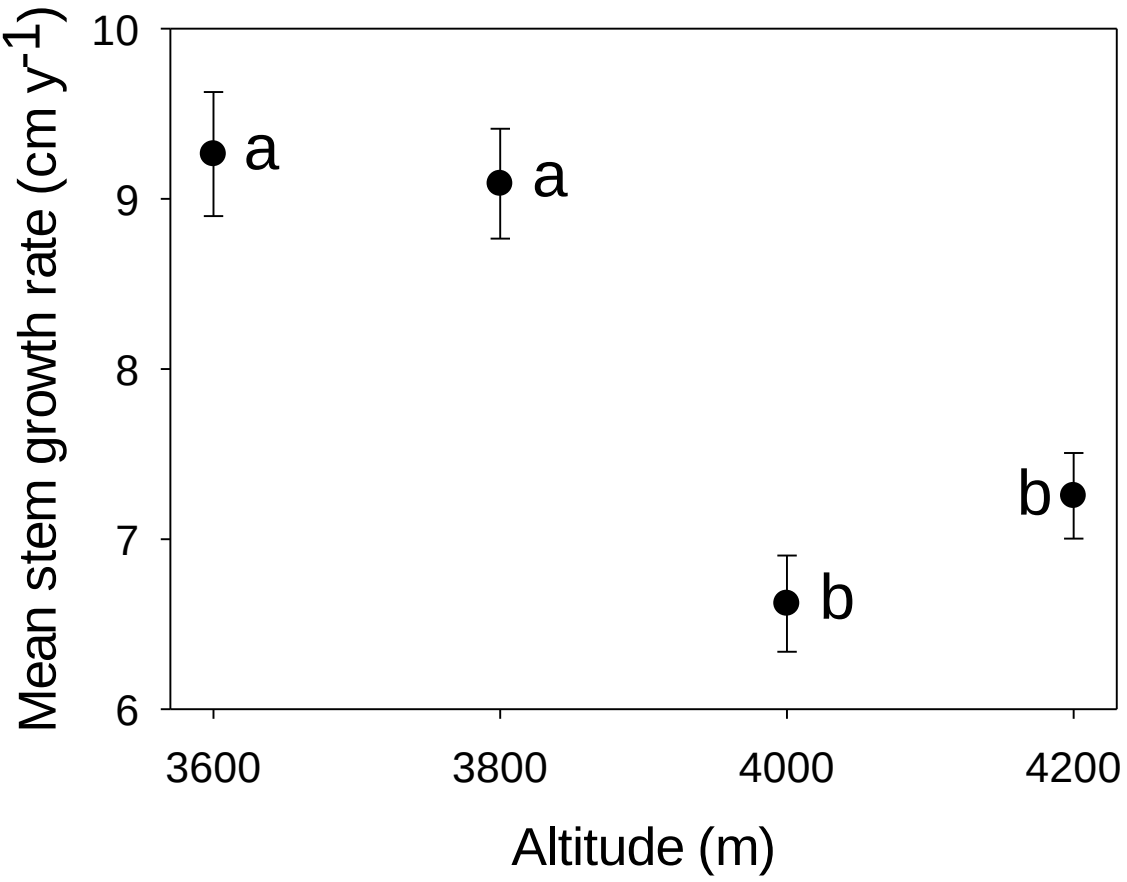
488 Fig. 2

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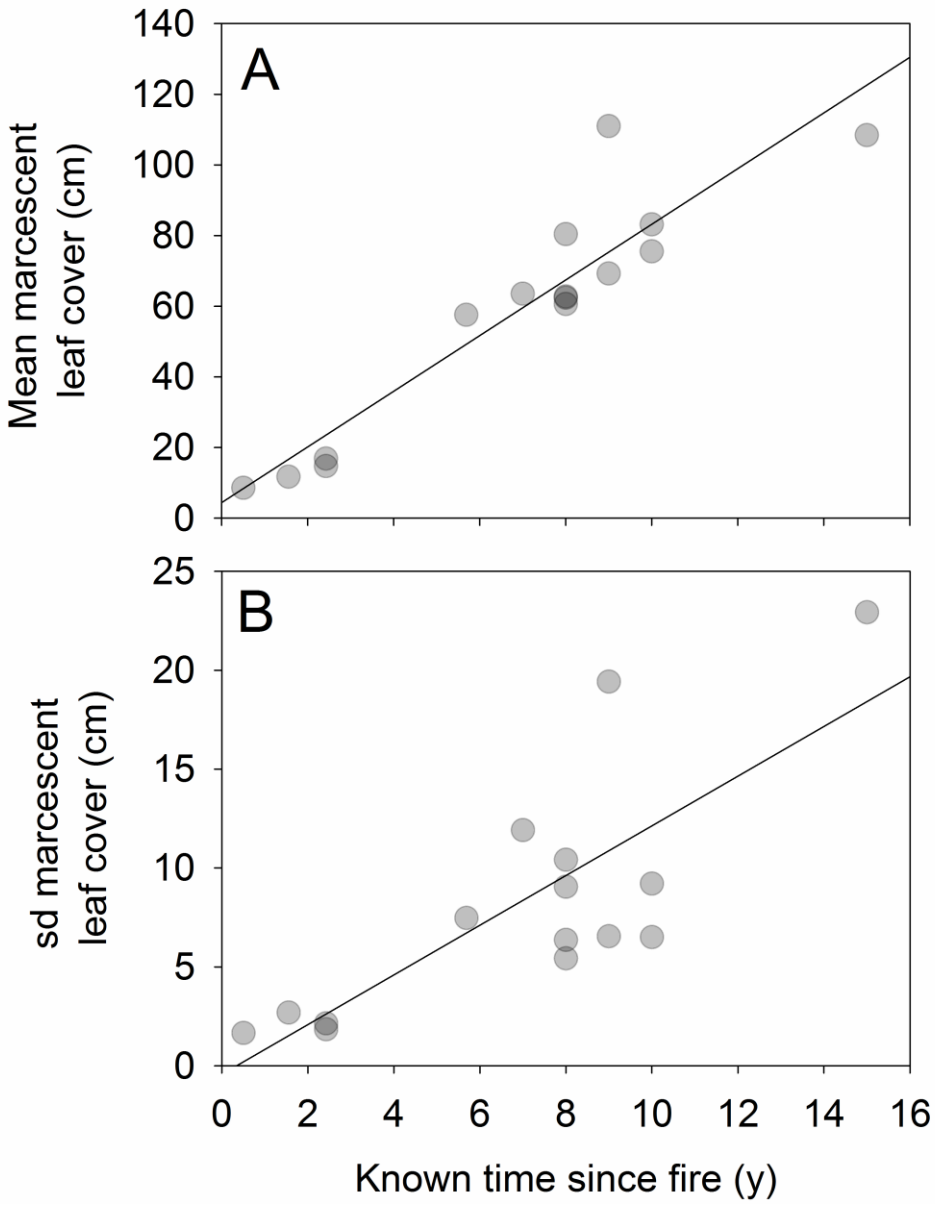
491 Fig. 3

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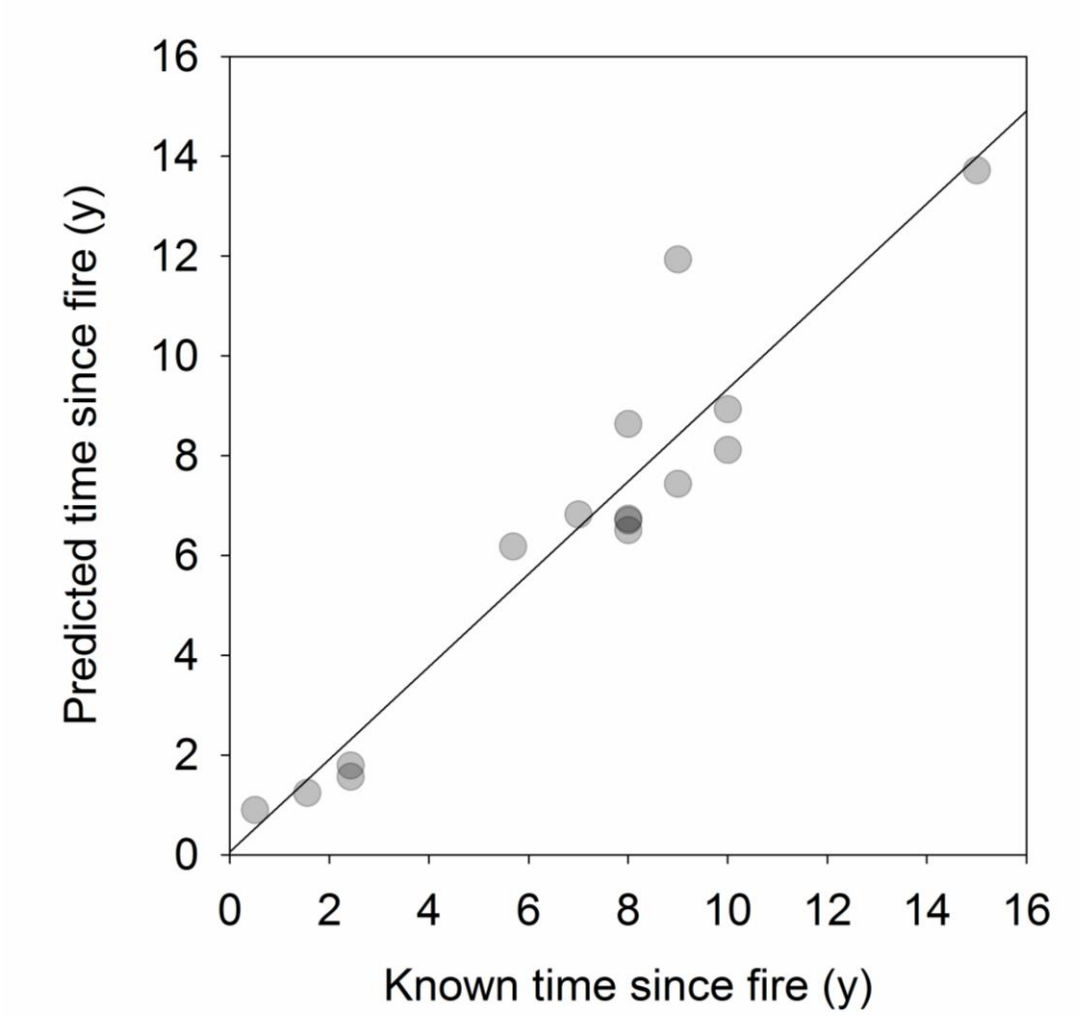
494 Fig. 4


Predicted time since fire (y)
Known time since fire (y)
0
2
4
6
8
10
12
14
16

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